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# THE AMERICAN NATURALIST

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VOL. XLV

February, 1911

No. 530

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## THE APPLICATION OF THE CONCEPTION OF PURE LINES TO SEX-LIMITED INHERI- TANCE AND TO SEXUAL DIMORPHISM<sup>1</sup>

PROFESSOR T. H. MORGAN

COLUMBIA UNIVERSITY

IN the same sense in which our ideas concerning variation and heredity have been entirely revolutionized since 1891, so has a similar change taken place in regard to our theories of sex determination. Sex is now treated by the same methods that are used for Mendelian characters in general. From this point of view I propose to consider to-day three questions, intimately associated. First, the treatment of sex as a Mendelian character; second, the relation between sex and the inheritance of secondary sexual characters; third, the bearing of the recently discovered cases of "sex-limited-inheritance" on the problem of the transmission of characters in general.

Most modern theorists are in agreement that the heredity of sex can be best understood when one sex is regarded as a pure line, or homozygous, and the other sex is treated as a phænotype, *i. e.*, as heterozygous. The experimental evidence has made it plain that in some animals and plants it is the female that is heterozygous, and in other animals and plants it is the male that is heterozygous. Hence have arisen through the necessities of the situation the two following classes of formulæ:

<sup>1</sup> From a symposium on "The Study of Pure Lines of Genotypes," before the American Society of Naturalists, December 29, 1910.

		Gametes	
♀♂ Female		♀	♂
♂♂ Male		♂	♂
		<hr/>	
		♀♂	♂♂
		female	male
♀♀ Female		♀	♀
♀♂ Male		♀	♂
		<hr/>	
		♀♀	♀♂
		female	male

In certain groups of animals, as in *Abraxas* amongst insects, and in poultry amongst birds, the first scheme is essential to an interpretation of the facts obtained by experiment. In other groups, as in *Drosophila* amongst insects, and in man amongst the vertebrates, the second scheme accounts for the experimental results.

These methods of formulation are open to two serious objections. As the tables show, the combination of ♀♂ stands for the female in one case, and for the male in the other. In order to avoid this apparent contradiction it is assumed that in some groups femaleness dominates maleness, and in other groups maleness dominates femaleness, which seems to me paradoxical at least.

It will be observed also that in the first of these schemes the male carries none of the sexual characters of the female, and in the second scheme the female carries none of those of the male; both of which assumptions do not seem to me to be completely in accord with fact. Cytologists represent these same two schemes in a different way. They represent in the one case the female character by X; and the male by the absence of X. Thus:

		Gametes	
XO Female		X	O
OO Male		O	O
		<hr/>	
		XO	OO
		female	male

This representation covers the first class of cases where the female is heterozygous. For the second class, where the female is homozygous, the following scheme is

used, in which the female is represented by two X's and the male by one X:

	Gametes	
XX Female	X	X
XO Male	X	O
	XX	XO
	female	male

The XO—OO scheme applies, as before, to the case of *Abraxas* and to poultry, and the XX—XO scheme to the other class of cases. The latter expresses also exactly what takes place in the chromosomes of those groups where two classes of sperm exist (in relation to the X element), as has been demonstrated by Stevens and by Wilson.

In both of these two latter schemes the production of the female is ascribed to the presence of the chromosome X, but in the first formula one X makes the female and its absence stands for the male, while on the second formulation two X's make the female, while one makes the male. In one case XO is female and in the other XO is male. Again we meet with the same paradox as in the first two formulations.

The chief drawback to these formulæ is, in my opinion, the absence of any character to stand for maleness. Absence of femaleness does not appeal to me as a sufficient explanation of the development of a male; for the male is certainly not a female minus the female characters.

Nevertheless, despite these objections I am inclined to think that these two methods of formulation indicate the direction in which we must look for an explanation of the experimental evidence, and that they may be still utilized provided we can so modify them that their inconsistencies can be made to disappear.

It seems to me that if we are to succeed in bringing sex into line with Mendelian methods we must be prepared to grant that there are representative genes for the male condition and others for the female; and we must so shape our formulæ that the female carries the

genes for the male and the male carries those for the female. In fact, I am inclined to think that the evidence forces us to accept Darwin's original view, that in each sex the elements of the other sex are present; a view that has been largely given up by modern theorists (except by Strasburger). I think that we must accept this interpretation for several reasons. Every zoologist is familiar with cases in which the same individual may at first function as a male and later as a female. More remarkable still is the case of the Nematodes in which in some species the female has come to produce both eggs and sperm as shown by Maupas and more recently by Potts, while in another closely related species it is probably the male, according to Maupas and Zur Strassen, that has come to produce eggs as well as sperm. There is further the class of cases where the female develops the male secondary characters and the male those of the female. This class of cases I shall discuss later, for the value of this evidence will turn on whether these secondary sexual characters are represented by independent genes, or are expressions of the presence of one or the other sexual condition; or due to a combination of these two possibilities.

By means of the following formulæ we can meet the requirements that the situation seems to me to demand. If we admit that in the first class one of the genes has become larger than the other female genes, and if we admit that in the second class one of the female genes has become smaller than its sister genes we can account for the results as the following formulæ show:

		Gametes	
Fmfm Female	fmfm Male	Fm fm	fm fm
		Ffmm female	ffmm male
FmFm Female	Fmfm Male	Fm Fm	Fm fm
		FFmm female	Ffmm male

It should be carefully observed that in this scheme the female genes, F or f pair when they meet (allelomorphs); likewise the male genes pair only with male genes. In fact, both genes are carried by all of the gametes. Sexual dimorphism may appear either because one female gene has become stronger than the others, or, because one has become weaker. On the first view we have the case where the female is heterozygous in its female genes; in the latter case it is the male that is heterozygous in its female genes. If in this latter case we assume that the weakened female gene is contained in the so-called Y-chromosome we can then understand how it is that we have a degraded series of this chromosome leading in some forms to its final extinction, for even its disappearance leaves the formulæ unaffected. On the same grounds we may anticipate that in those species in which the X elements are alike in the male, one X in the female may be found larger than its partner, although visible size differences in the chromosomes are not essential to the scheme, since these chromosomes undoubtedly contain many other factors than those of sex whose presence might obscure size relations even when such exist in the sex genes.

These formulæ appear more complicated than those previously given, but in reality they are not so. It is the presence of m in all of the gametes that gives the appearance of complication. If this is omitted, as in the formula given below, the formulæ are no more complex than those given earlier.

	Gametes	
Ff Female	F	f
ff Male	f	f
	<hr/> Ff	<hr/> ff
FF Female	F	F
Ff Male	F	f
	<hr/> FF	<hr/> Ff

The formulæ might be further simplified, if it seemed desirable to do so, by simply indicating the determining factor in each case as shown below; thus:

	Gametes	
FO Female	F	O
OO Male	O	O
	FO	OO
OO Female	O	O
Of Male	O	f
	OO	Of

But this last simplification is misleading, if the thesis that I shall here maintain in connection with sex-limited inheritance is correct; because the F's and the f's omitted in the last case are supposed to be carried in definite bodies, the chromosomes, which also carry other factors than sex factors, and it is essential to indicate their presence in some way in order that these other factors may have some means of transportation.

In a recent paper on sex determination in phylloxerans and aphids (1909) I discussed at some length different theories of sex determination, and adopted provisionally the view that the outcome is determined by a quantitative factor. The present hypothesis is little more than a further development of this same view,<sup>2</sup> but I hope in a form more in accord with the Mendelian treatment of the problem. Sex is still represented as the result of a quantitative factor F (or f), but its relation to the male factor is now expressed, for maleness is not assumed, as before, to be no femaleness or less femaleness. Here, as there, more of a particular factor turns the scale towards femaleness in the first class of cases, and less of the female factor allows the scale to turn in the opposite direction in the second class of cases.<sup>3</sup>

<sup>2</sup> In 1903 I suggested that in the case of the bee a quantitative factor determines sex, viz., the chromatin; two nuclei producing a female and one a male. Wilson (1905) has identified the quantitative factor with a special chromosome and this interpretation of the quantitative factor is here followed. On Wilson's view the male condition is represented by the absence of the X-chromosome in some cases, and by the presence of only one X-chromosome in the others, (see ante); but on my view the determination of sex is regulated by this quantitative factor in relation to another factor, the male determining element.

<sup>3</sup> It should be pointed out that these formulæ are in no way related to a suggestion that I made in 1907 in regard to dominance and recessiveness

These formulæ have certain advantages over those now in vogue, first, because the male gene is not ignored as a factor in sex determination; second, that its presence, both in males and females, explains how under certain conditions the male or the female may assume some of the characters of the opposite sex; third, that the paradox of the female being the heterozygous form in one class and the male in the other class is, in part at least, resolved; fourth, that the ease with which species pass from the hermaphrodite condition to that of sexual dimorphism and the reverse is understandable; fifth, that the production of males by parthenogenetic females can be accounted for by the loss of one of the female genes in the polar body; and lastly, we see how there may be two kinds of eggs, as in *Dinophilus apatris*, both of which can be fertilized; for, in such cases the spermatozoa should be all alike.

I do not wish to urge this view too positively, for I am acutely aware that we are only at the beginning of our understanding of the problem of sex determination, but I believe that the difficulties of the current hypotheses must be clearly understood and met if possible.<sup>4</sup>

#### THE INHERITANCE OF SECONDARY SEXUAL CHARACTERS

From the point of view reached in the preceding discussion let us now examine the problem of the inheritance of secondary sexual characters.

Males are distinguished from females not only by the presence of sperm in place of eggs, but by the presence in general. That view I have entirely abandoned. In the present hypothesis the relation of the determining elements is stated in the same form as in other Mendelian formulæ, with the possible exception that here one gene is represented as larger or smaller than its allelomorphs, and the scale is turned by the mass relation between these female genes and those of the male.

<sup>4</sup>I have not discussed here the possibility of selective fertilization, because if we can explain the facts without this problematical assumption we simplify the problem greatly. Moreover, the evidence brought forward by Payne, Brown and myself, while admittedly insufficient, stands definitely opposed to the view of selective fertilization.



of different kinds of ducts, glands, copulatory organs, or other accessory sexual apparatus; and also by structures not essential to reproduction. These last we call the secondary sexual characters.

It has long been known that in the embryonic development of the vertebrates some of the accessory organs of the male appear in the female, and conversely some of the accessory organs of the female in the male. This evidence seems to me to point with no uncertain meaning to the conclusion that each sex carries the genes of the other. It is however the secondary sexual characters rather than these accessory organs of which I wish to speak now; for, these often appear to be present in one sex only. Are these characters represented in all eggs and sperm or are they by-products of the sexual condition of the animal? Fortunately there is a good deal of *experimental evidence that bears on this question*, but it is also true that the evidence teaches that the matter must be handled with care, and if I seem to speak dogmatically it is for lack of time rather than for want of caution.

It has been shown by Meisenheimer that removal of the gonads of the caterpillar of *Ocneria dispar* fails to produce any effect, or very little, on the secondary sexual characters of the moth. It would seem, therefore, that these characters are represented in the germ cells in the same way as are other characters, and are not dependent for their development on the presence of the gonads. Some mechanism must exist by means of which the genes of these organs are distributed so that two kinds of individuals are produced. It has been suggested by Castle that the secondary sexual characters may be carried by the Y-element in the formulæ  $XX = \text{female}$ ,  $XY = \text{male}$ , but this hypothesis fails to explain the results when the Y-element is absent, as E. B. Wilson has pointed out. It also fails to explain how the male secondary sexual organs can appear in the female after castration.

On the sex formulæ that I have suggested it is possible to account for the results, if the genes for these

characters are carried by all cells alike; possibly they go along with the male-group, but this is not essential. Whether they *develop*, or not, will depend on the presence of other genes in the cells. Thus when the Fmfm group is present they will be suppressed, or when, as on the other formulæ, the FmFm group is present. We can understand on this view why in the insects the male secondary sexual organs do not develop in the female after removal of the ovaries, because in this group it is not material derived from this source, but from materials produced in the cells themselves, that bring about the suppression.

It has been demonstrated by Geoffroy Smith that when the young males of the spider crab, *Inarchus mauritanicus*, are infested by *Sacculina* the secondary sexual characters of the female develop. It appears that the parasite produces some substance that inhibits the activity of the male-producing group in each cell, or counteracts some materials produced there, so that the female characters now find the situation favorable for their development. When the young female crab is infected by *Sacculina* she does not develop the male secondary characters, which is in harmony with the view just stated for the manner of action of the parasite.

In birds and in mammals it has long been recognized that some substance is produced in the ovary that inhibits the development in the female of the male secondary sexual characters, for, after removal of the ovaries the male characters may *to some extent* develop. It seems fairly clear that here the female group in each cell fails to entirely suppress the male characters; the inhibiting effect from this source must be reinforced from something produced in the ovary. Whether after castration of the male the secondary sexual characters of the female develop is not so clear, since some at least of the characters that characterize the castrated male may be juvenile. But on my view the possibility exists for the castrated male to produce the secondary sexual

characters of the female, if their development is in part suppressed by substances made in the testis.

The view here presented also allows us to explain how the secondary sexual characters of the male are transmitted through the female, as they may be so transmitted.

#### THE INHERITANCE OF SEX-LIMITED CHARACTERS

In recent years a new class of facts has been discovered that promises to throw a flood of light not only on the sex-determination problem, but also on the problem of inheritance in general. I refer to the cases of sex-limited inheritance.

We mean by sex-limited inheritance that in certain combinations a particular character appears in one sex only. An example will make this clear. In one of my cultures of the red-eyed fly, *Drosophila*, a white-eyed male appeared. Bred to red-eyed females, all of the offspring, male and female alike, had red eyes. These inbred produced red-eyed males and females, and white-eyed males. In other words the white-eyed mutant transmitted his character to half of his grandsons, but to none of his granddaughters.

Yet this white-eyed condition is not incompatible with femaleness; for, it can be artificially carried over to the female by making a suitable cross. If, for instance, a white-eyed male is crossed with a heterozygous red female, there will be produced red-eyed males and females and white-eyed males and females.

There are certain combinations of sex-limited characters that give results outwardly similar to sexual dimorphism. If a black langshan cock is crossed to a dominique hen, all of the sons are barred and all of the daughters are black. If a white-eyed *Drosophila* female is crossed with a red male all of the sons will have white eyes, and all of the daughters will have red eyes. I have another strain of these flies with *small wings* and still another strain with *truncated wings*. If a female of the former is crossed with a male of the latter strain all of

the daughters will have *long wings* and all of the sons will have *small wings*, like their mother.

These cases conform to Mendel's principle of segregation. Were there time I could show by an analysis of the problem why these sex-limited characters behave in inheritance in a different way from secondary sexual characters, although the results in both cases may be accounted for on the assumption that there are genes in the cells for both kinds of characters. In a word, this difference exists because one of the factors for the sex-limited characters in question is absent from one of the *female determining chromosomes*, while the genes for the secondary sexual characters of the male are contained in other chromosomes, possibly in those that contain the male determinants.

This interpretation of the relation between the X-chromosomes and sex-limited characters makes it now possible to demonstrate a point of great theoretical importance. I invite your serious attention for a few moments longer to this question. Three other characters have appeared in my cultures that are sex-limited; one of these only I may now speak of. A male with wings half the normal length suddenly appeared. He transmitted his short wings to some of his grandsons, but to none of his granddaughters. I tried to see if the other sex-limited character, white eyes, could be combined in the same individual with short wings. As the next diagram shows a red-eyed short-winged male was bred to a white-eyed female with normal wings. All of the offspring had long wings; the female had red eyes and the males white eyes. These were inbred and produced white and red-eyed males and females with long wings, red-eyed males with short wings, and white-eyed males with short wings. In the last case the transfer had been made. The reciprocal cross also given in the diagram is equally instructive.

LWF	—	LWF	Long-winged, white ♀	
SRF	O	Short-winged, red ♂		
<hr/>				
LWFSRF — LWF				
LWF	SRF	SWF	LRF	♀ Gametes
	LWF — O			♂ Gametes
LWFLWF	Long-winged	♀	white eyes	
SRFLWF	Long-winged	♀	red eyes	
SWFLWF	Long-winged	♀	white eyes	
LRFLWF	Long-winged	♀	red eyes	
LWF	Long-winged	♂	white eyes	
SRF	Short-winged	♂	red eyes	
SWF	Short-winged	♂	white eyes	
LRF	Long-winged	♂	red eyes	
LRF	LRF	Long-winged, red ♀		
SWF	O	Short-winged, white ♂		
<hr/>				
LRFSWF — LRFO				
LRF	SWF	LWF	SRF	♀ Gametes
	LRF	O		♂ Gametes
LRFLRF	Long-winged	♀	red eyes	
SWFLRF	Long-winged	♀	red eyes	
LWFLRF	Long-winged	♀	red eyes	
SRFLRF	Long-winged	♀	red eyes	
LRF	Long-winged	♂	red eyes	
SWF	Short-winged	♂	white eyes	
LWF	Long-winged	♂	white eyes	
SRF	Short-winged	♂	red eyes	

In both cases the combination is possible because in the female of the hybrid ( $F_1$ ) a shifting of the gene for long and that for short wing (both carried by the X-chromosome) takes place. This interchange is possible during the synezeisis of the two X-chromosomes. On the other hand the male contains only one X-chromosome which has no mate, hence the gene for long wings in the hybrid ( $F_1$ ) can not leave that chromosome to pass into the male-producing group. If it could do so short-winged females would also appear, but as I have shown they are not present in the second generation.

Interpreted in terms of chromosomes these results can have, in my opinion, but one meaning. During union of homologous chromosomes (during synezeisis, perhaps) homologous genes pair and later separate to move to op-

posite sides (or enter the chromosome sometimes one way and sometimes the other). All the genes contained in the X-chromosomes can thus shift in the female because in this group two X's are present. Sex-limited inheritance is only possible where similar conditions exist (either in the male or in the female) and since in man color blindness follows the same scheme as does white eyes in my flies, we have an experimental proof that in the male of homo sapiens there is only one X-chromosome, and this, in fact, Guyer has just shown to be the case from cytological evidence. But by parity of reasoning it is the female in *Gallus bankiva* that should have only one X present, but Guyer is persuaded that here too (at least in the race of fowls he studied) the male has only one X-chromosome. There is then in this case a contradiction between the experimental evidence and that furnished by cytology and it remains to see which is correct.

Bateson has shown that some of these cases of sex-limited inheritance can be explained on the grounds that there is a repulsion between the female-determining factor and that character that is sex-limited. The view that I maintain does not involve the idea of a repulsion between unlike elements, not allelomorphic. Spillman's hypothesis also involves this idea of repulsion between unlike elements. On my view, on the contrary, an attempt is made to show how the results may be due to a connection existing between certain material bodies in the egg; a connection that is consistently carried through successive generations, and subject only to the ordinary interchange of genes between homologous chromosomes (when a pair of chromosomes is present).<sup>5</sup>

For several years it has seemed to me that the chromosome hypothesis, so called, could not be utilized to explain the Mendelian results in the form presented by

<sup>5</sup> The hypothesis advanced here to explain sex-limited inheritance applies also to *Abraxas* if the latter follows the Fmfm scheme and if *in the egg* there is no interchange between the F-bearing and the f-bearing chromosomes.

Sutton, because, if it were true, there could be no more Mendelian pairs in a given species than the number of chromosomes present in that species. Even if this objection could be avoided<sup>6</sup> the more serious objection still remained, namely, that with a small number of chromosomes present many characters should Mendelize together, but very few cases of this sort are known. De Vries was the first, I believe, to point out that this objection could be met if the genes are contained in smaller bodies that can pass between homologous pairs of chromosomes; and Boveri has admitted this idea as compatible with his conception of the individuality of the chromosomes. In the case of the inheritance of two sex-limited characters in the same animal we have an experimental verification of this hypothesis.

<sup>6</sup> Spillman's suggestion that the difficulty exists only when it can be shown that more dominant characters can occur in the same individual than the number of chromosomes seems to me only to push back the difficulty.